Quasi-stationary distributions for a model of populations adapting to a changing environment

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Summary

Presentation of the model

Exponential quasi-ergodicity

Interpretation

Presentation of the model

Exponential quasi-ergodicity

Interpretation

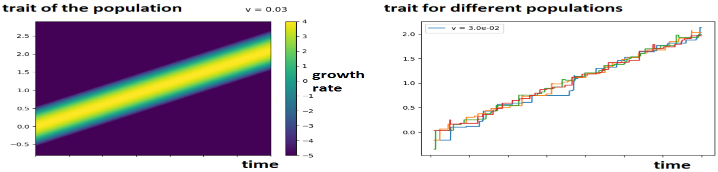
A system of coupled equations

$$(S)\begin{cases} X_t = x - v\ t + \sum_{T_i \leq t} W_i, \\ \quad \text{the phenotypic lag} \\ N_t = n + \int_0^t \left(r(X_s)\ N_s - c_p\ (N_s)^2\right) ds + \sigma \int_0^t \sqrt{N_s}\, dB_s, \\ \quad \text{the size of the population} \\ \qquad\qquad \text{while } t \leq \tau_\partial, \end{cases}$$

where extinction is given by $\tau_\partial := \inf\{t,\ N_t = 0\}$:

The moving optimum model

Profile for fitness unimodal, in translation with constant speed v



For simplicity, we assume that population is always homogeneous:

$\Rightarrow$ more suited for asexual populations

$\Rightarrow$ we neglect fixation time

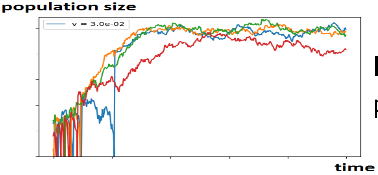
Why an ecological dynamics

- Increased extinction rate for maladapted populations
  $\Rightarrow$ A second level of natural selection
  since we will only consider surviving populations
- Lower population size for maladapted populations
  $\Rightarrow$ fewer mutations occur

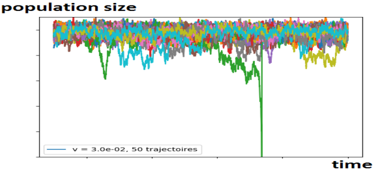
Assumption : on a broader time scale compared to fixation
(the first level of natural selection)

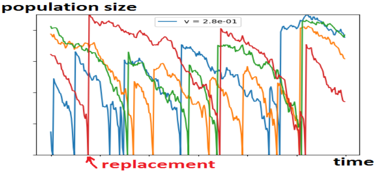
Ecological dynamics

The Feller logistic model for the population size $(N_t)_{t \geq 0}$



Exponential growth of surviving populations





Stability around some carrying capacity

Declining population : growth rate not sufficient to persist

A system of coupled equations (bis)

In the case f is bounded, our model can be described this way :
Let $M = \{T_i\}_{i\geq 1}$ be a Poisson Point Process with intensity $\|f\|_\infty$,
$(W_i)_{i\geq 1} \sim \nu(dw)$ be iid rv (effect of the mutations),
$(U_i)_{i\geq 1} \sim \mathcal{U}([0,1])$ be iid rv (filtering of the Point Process)

$$(S) \begin{cases} X_t = x - v\ t + \sum_{T_i \leq t} \mathbf{1}_{\left\{U_i \leq \frac{1}{\|f\|_\infty} f(N_{T_i})\, g(X_{T_i^-}, W_i)\right\}} W_i, \\ \quad \text{the phenotypic lag} \\ N_t = n + \int_0^t \left(r(X_s)\ N_s - c_p\ (N_s)^2\right) ds + \sigma \int_0^t \sqrt{N_s}\ dB_s, \\ \quad \text{the size of the population} \\ \qquad \text{while } t < \tau_\partial, \end{cases}$$

where extinction is given by τ_∂:

- as soon as N reaches 0
- or as soon as X escapes $]-L, L[$

Evolutionary dynamics (1)

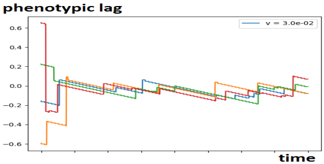
- $(X_t)_{t \geq 0}$: gap relative to the moving optimum
  $\Rightarrow$ translation at speed v without mutations
- Point Process describes the arrival of mutations that fix
  - rate for a mutation $W \in dw$ $(X_{t-} \to X_{t-} + W)$:
    product $f(N_t) \times g(X_{t-}, w) \times \nu(dw)$

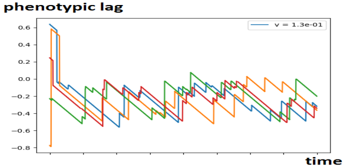
$\nu(dw)$: profile of mutations occurring in one individual
$g(X_{t-}, w)$: probability of fixation
$f(N_t)$: rate for the arrival of a mutation in the whole population
$\to f(n) = C\, n$ is a natural assumption

  - Markov process : no other dependency on the past
    $\Rightarrow$ Poisson Point Process

Evolutionary dynamics (2)

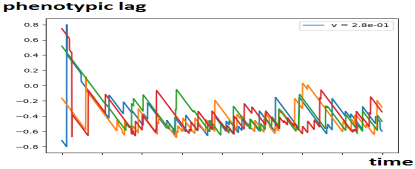
Different regimes visible for the gap relative to the moving optimum :





Population naturally adapting : little risk of extinction

Intermediate regime



The bias of considering surviving populations explains its apparent adaptation

Presentation of the model

Exponential quasi-ergodicity

Interpretation

Convergence to some unique QSD

Main result :

Convergence with exponential speed to a unique QSD α, uniformly over the initial condition :

$$\exists C > 0, \zeta > 0,\ \forall \mu \in \mathcal{M}_1\big((-L,\, L) \times \mathbb{R}_+^*\big),\ \forall t > 0,$$

$$\|\mathbb{P}_\mu\left((X,\, Z)_t \in (dx,\, dz) \mid t < \tau_\partial\right) - \alpha(dx,\, dz)\|_{TV} \leq C\, e^{-\zeta t}$$

$\tau_\partial := \inf\{t > 0,\ Z_t = 0\} \wedge \inf\{t > 0,\ |X_t| \geq L\}$
Coupling estimate relying on a procedure introduced by N. Champagnat and D. Villemonais [1]

Sufficient conditions

- No deleterious mutation can fix :
  $|x+w|<|x| \Leftrightarrow g(x,w)>0$, otherwise $g(x,w)=0$
- symmetry and regularity conditions
- lower-bounds for f, g and ν to ensure that some mutations will indeed occur and make the phenotypic lag diffuse
- g is bounded by 1, ν a probability measure.
- No critical value for the environmental change v.

Presentation of the model

Exponential quasi-ergodicity

Interpretation

a QSD, what does it mean?

- α QSD $\Rightarrow$ left eigenvector for the transition semi-group, ie

$$\forall\, t > 0,\ \forall\, h, \quad \mathbb{E}_\alpha \left[h(X_t,\, Z_t)\,;\ t < \tau_\partial\right] = e^{-\lambda_0\, t} \int h(x,z)\, \alpha(dx,\, dz)$$

- λ_0 : extinction rate $\rightarrow \forall\, t > 0,\ \mathbb{P}_\alpha(t < \tau_\partial) = e^{-\lambda_0\, t}$

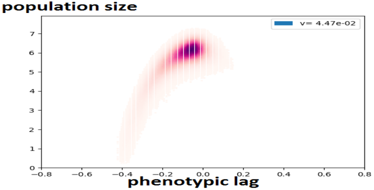
- the "long term surviving capacity" :

$$\frac{\mathbb{P}_{(x,\,z)}(t < \tau_\partial)}{\mathbb{P}_\alpha(t < \tau_\partial)} \underset{t \to \infty}{\longrightarrow} \eta(x,z)$$

- η right eigenvector for the transition semi-group, ie

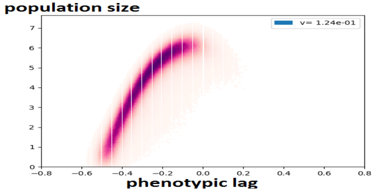
$$\forall\, t > 0,\ \forall\, \mu, \quad \mathbb{E}_\mu \left[\eta(X_t,\, Z_t)\,;\ t < \tau_\partial\right] = e^{-\lambda_0\, t} \int \eta(x,z)\, \mu(dx,\, dz)$$

Profiles of the QSD α

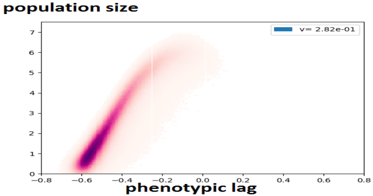


Adaptation with little effect of extinction

$$\mathbb{P}_{(x,z)}\left[(X,Z)_t \in (dx,dz) \,\middle|\, t < \tau_\partial\right] \underset{t\to\infty}{\longrightarrow} \alpha(dx,dz)$$

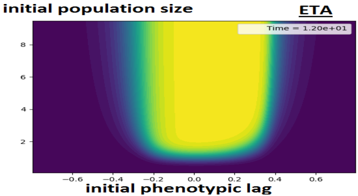


Intermediate regime



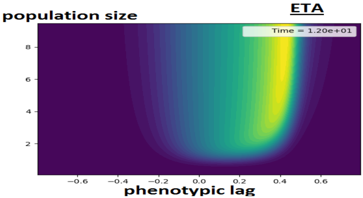
Adaptation strongly linked to extinction

Profiles of the "long term surviving capacity"

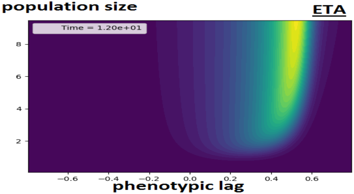


Adaptation with little effect of extinction

$$\eta(x,z) := \lim_{t\to\infty} \frac{\mathbb{P}_{(x,z)}(t < \tau_\partial)}{\mathbb{P}_\alpha(t < \tau_\partial)}$$



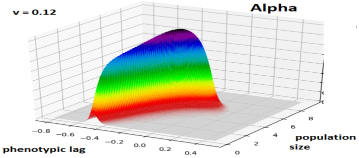
Intermediate regime



Adaptation strongly linked to extinction

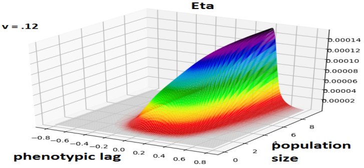
Perspectives

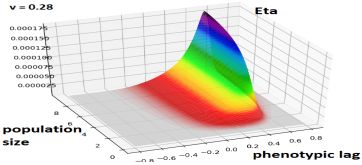
- Include more realism in the model
  - Case $X \in \mathbb{R}$, behavior for $L \to \infty$?
  - Include deleterious mutations
  - More general changing environments
    $\Rightarrow$ uniform bound over some class of functions : $t \mapsto E_t$
    (the presented model corresponds to $E_t^0 := v\, t$)
- Description of the QSD
  - Regularity of the QSD : some density solution of a non-local EDP
  - Derivative of the QSD according to its parameters
- Convergence of the empirical profile of mutations to some deterministic profile (depending on α and η)



Thank you for your attention

I'll be pleased to answer your questions





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- Champagnat N and Villemonais D, Exponential convergence to quasi-stationary distribution for one-dimensional diffusions,ArXiv e-prints, June 2015.
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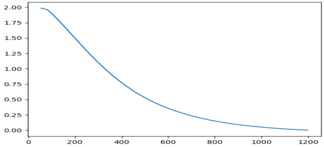
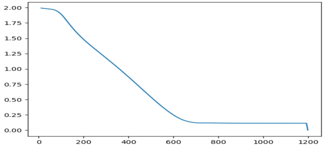
- Nassar E, thèse : Modèles probabilistes de l'évolution d'une population dans un environnement variable, sous la direction de Kopp M et Pardoux E, 2016
- Nassar E, Pardoux E : On the long time behavior of the solution of an SDE driven by a Poisson Point Process, to appear inJournal of Applied Probability

Supplementary material

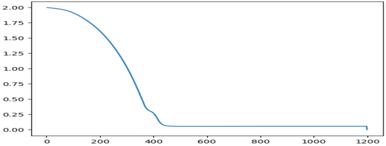
Convergence in total variation towards the QSD





Population naturally adapting : little risk of extinction

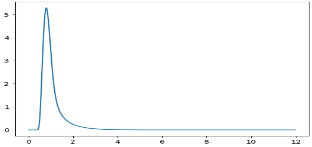
Intermediate regime



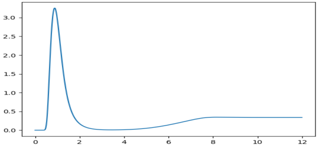
Mortality dominates

Convergence of the mortality rate

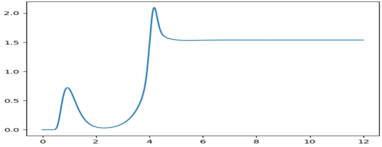
Different regimes visible for the gap relative to the moving optimum :



Population naturally adapting : little risk of extinction

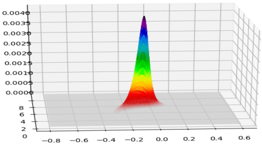


Intermediate regime

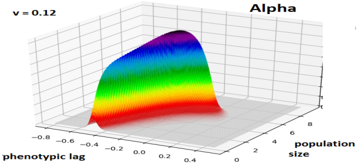


Mortality dominates

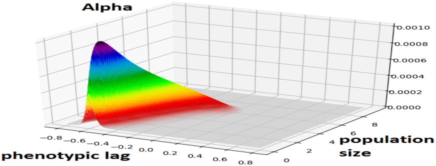
3D view of the QSD



Population naturally adapting : little risk of extinction

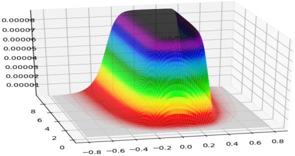


Intermediate regime

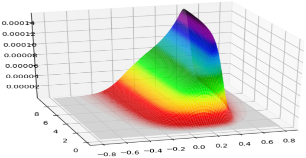


Mortality dominates

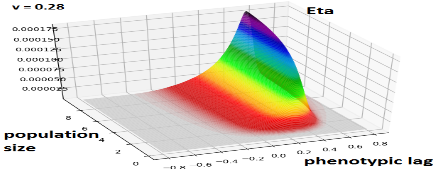
3D view of the capacity of survival



Population naturally adapting :
little risk of extinction

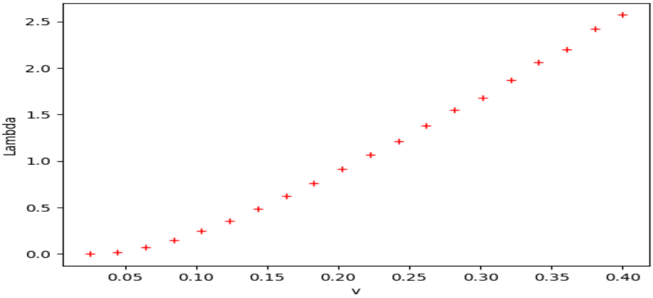


Intermediate regime



Mortality dominates

rate of extinction as a function of environmental change



Two criteria to justify

General set-up given by N. Champagnat and D. Villemonais [1]

Choose α_c (the coupling measure) such that:
(A1) there exists $t_1 > 0$, $c_1 > 0$ such that :

$$\forall v \in \mathcal{V}, \quad \mathbb{P}_v(V_{t_1} \in dv \mid t_1 < \tau_\partial) \geq c_1 \, \alpha_c(dv)$$

(A2) there exists $t_2 > 0$, $c_2 > 0$ such that :

$$\forall v \in \mathcal{V}, \, \forall t \geq t_2, \quad c_2 \, \mathbb{P}_v(t < \tau_\partial) \leq \mathbb{P}_{\alpha_c}(t < \tau_\partial)$$

in our model

1. $V_t = (X_t, Z_t)$
2. $\mathcal{V} =]-L, \, L[\times\mathbb{R}_+$